

Visual Motion Perception at the Time of Saccadic Eye Movements and its Relation to Spatial Mislocalization

CHOONGKIL LEE AND JUNGAH LEE

Department of Psychology, Seoul National University, Kwanak, Seoul, Korea

ABSTRACT: The same retinal image motion can be produced by a variety of combinations of eye and target motion. In natural conditions, extraretinal information disambiguates retinal information for motion perception. By controlling the timing of visual motion with respect to saccades, it was possible to appraise the roles for motion perception of the signal related to saccades occurring in the vicinity of visual motion. When a visual motion was seen before or after a saccade, its perceived direction was biased in the direction opposite to the saccade. The magnitude of the bias depended on the timing of the visual motion with respect to the saccade and the meridian of the visual motion. The bias appears to be independent of the deformation of visual space reported to occur before and after saccades.

KEYWORDS: spatial localization; perceptual anisotropy; efference copy; oblique effect

INTRODUCTION

Experimental studies suggest that visual perception is subject to a nonstationary change around saccadic eye movements. The same retinal inputs lead to differential perception depending on occurrence of saccades. A notable example is spatial mislocalization, where spatial localization of a visual target presented around a saccadic eye movement is biased.¹ When the target is presented before saccades, the two-dimensional pattern of mislocalization is compressive toward the spatial locus of saccade goal,² whereas it is expansive for targets presented after saccades.³ FIGURE 1 shows a schematic rendition of changes in perceptual space suggested by these studies. The rectilinear grid representing a part of perceptual space is warped to capture the main suggestions of experimental findings. We would like to caution, however, that this rendition is only to show the suggested deformation of visual space, and that its details, such as symmetry, magnitude, or boundary of deformation, are not known and not included in it.

We have investigated similar dynamic changes in motion perception at the time of saccadic eye movements, and their relation to spatial mislocalization.³⁻⁵ The

Address for correspondence: Choongkil Lee, Department of Psychology, Seoul National University, Kwanak, Seoul, Korea 151-742. Voice: +82 2 880 6440; fax: +82 2 875 2432. cklee@snu.ac.kr

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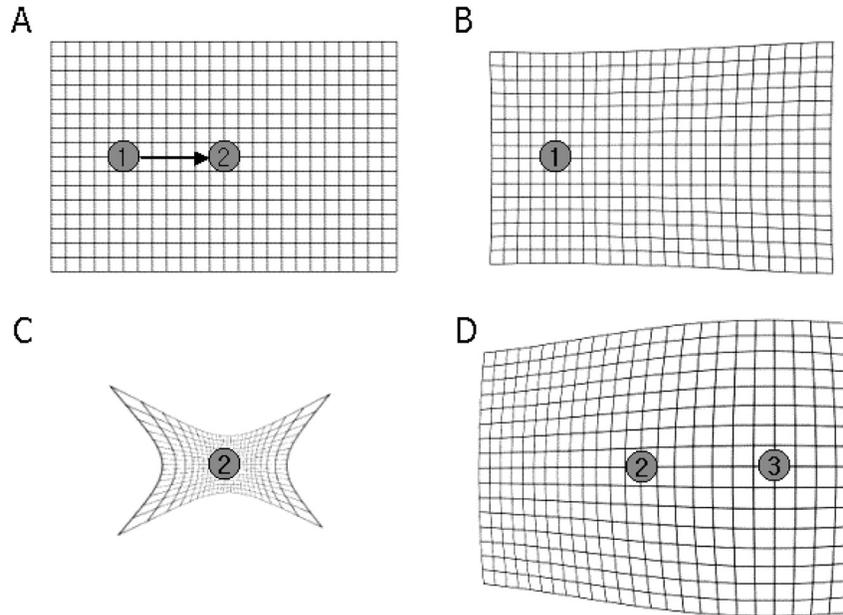


FIGURE 1. Changes in perceptual space around a saccade. (A) Loci of start (“1”) and end (“2”) of a saccade on a rectilinear grid representing an isometric perceptual space. (B) Fixation at “1” causes a variable shrinkage toward the fixation locus. (C) Immediately before the saccade from “1” to “2,” perceptual space compresses toward “2.” Although the pattern shown here is symmetrical about “2,” the compression of visual space to the right of “2,” in the direction of the saccade, is probably stronger.² (D) Immediately after the saccade, it expands from “3.” The origin of the expansion is shifted in the direction of saccades. Compression of visual space before saccades is probably larger in its magnitude than expansion after saccades.

same retinal image motion can be produced by a stationary eye seeing a moving target, by a moving eye seeing a stationary target, or by an appropriate combination of moving eye and target. This suggests that extraretinal information such as signals related to occurrence of eye movement are integrated for successful recovery of true target motion, because we have no trouble in doing so. Because extraretinal information deforms perceptual space, motion perception may also be nonveridical around saccades. By controlling the timing of visual motion with respect to saccades, we were able to dissociate the eye and target motions and appraise roles of the signal related to occurrence of saccades for motion perception.

EXPERIMENTAL PARADIGM

The goal of these experiments was to determine the perceived direction of a visual target presented immediately before and after a saccade. Human subjects with normal (or corrected to normal) vision participated. They were seated facing a 2-m

× 2-m frontal rear-projection screen at a distance of 115 cm. The head was stabilized with a bite bar. Horizontal eye position was measured with the infrared reflection method (Iris, Skalar Medical). A laser beam was deflected by a two-axis galvanometer scan head (model Z1913, General Scanning) and projected onto the screen, appearing as red spots of light 0.2 deg in diameter. Horizontal eye positions and horizontal and vertical positions of the laser beam were sampled at 500 Hz with a resolution of 12 bits, and stored for off-line analysis.

After a tone signaled the start of a trial, a spot of light was presented at a predetermined locus, on which the subject was instructed to maintain fixation. With a random delay after the eye entered an electronic window centered about the fixation point, the spot of light disappeared and briefly reappeared as a saccade target for 50 ms at a predetermined locus. With a variable delay after the saccade target disappeared, a tone signaled the subject to make a saccade to the remembered locus of the saccade target. Before or after the saccade, the laser spot completed a centrifugal sweep of 10° at the velocity of 125 deg/s. The timing of visual motion presented during the presaccadic period varied with respect to saccade onset, whereas the postsaccadic period was fixed with respect to saccade offset. Under the conditions of this experiment, the detection threshold for motion of the laser sweep is somewhere between 200 and 250 deg/s, and beyond this, the sweep appears as a line segment instead of a moving spot.⁴ The direction of target motion was pseudorandomly varied in steps of 5° between 45° and 135° , with 0° to the right and 90° straight up. The subject was then asked to match the direction of the laser sweep with a radial line segment produced by the same laser rapidly moving back and forth between the center of the screen and a point at 10° eccentricity. By manipulating a momentary dial switch on a hand-held response box, the subject was able to rotate the orientation of the line segment until it matched the perceived direction of the laser sweep. Pressing a button on the response box entered the final orientation of the line segment and started the next trial.

VISUAL MOTION PERCEPTION AROUND SACCADÉ

When a centrifugal sweep of a laser beam starting from the fixation point was seen by stationary eyes, the accuracy of its perceived direction depended on the inclination of the sweep: perception was imprecise for oblique directions compared to cardinal directions. When the same visual motion was seen around saccades, its perceived direction was systematically biased in the direction opposite to the saccade. It appeared that this bias was not produced by peripheral mechanisms such as eye drift, transient lens motion, or torsional eye movements, but by a central mechanism.⁴ Because visual space is distorted around saccades, as shown in FIGURE 1, we wondered whether this bias in motion perception is related to spatial mislocalization around saccades. However, this perceptual bias was not explained by spatial mislocalization. The configuration constructed from the mislocalized loci along the trajectory of the visual motion (FIG. 2) did not correspond to the pattern of the bias in motion perception,³ suggesting that saccade-related signals interact with perceptual processes at multiple sites.

A recent study further examined perceived direction of visual motion seen immediately before saccades, and found that in addition to perceptual bias in the direction

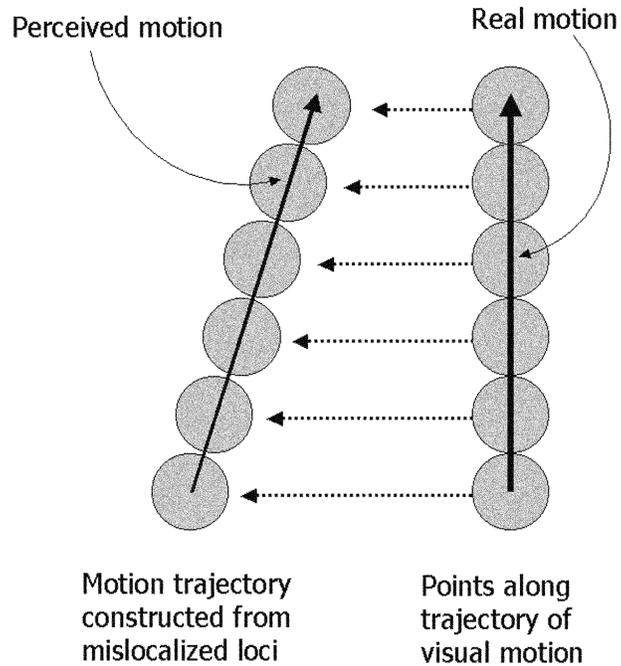


FIGURE 2. A wrong scheme. If one assumes visual motion as the successive appearance of single-point stimuli along the motion trajectory, the perceived motion around a saccade would be precisely predicted by the trajectory of spatially mislocalized positions of each point stimulus.

opposite to the saccade, perception of oblique direction becomes near veridical for presaccadic visual motion.⁵ The pattern of modulation of motion perception by a saccade-related signal reveals multiple processes with different time courses.

REEVALUATION OF THE SUBTRACTION SCHEME

It has been hypothesized that despite eye movements a stable perception of the space is maintained by algebraically subtracting an extraretinal eye position signal (EEPS) from the retinal information. Thus,

$$\Delta\text{Visual Perception} = \Delta\text{Retinal Information} - \Delta\text{EEPS}.$$

This subtraction predicts perceptual changes coincident with eye movement in direct relation to saccade amplitude and direction. However, one characteristic of the results from the studies examining perceptual changes around saccades is their inconsistency with the pattern predicted by the preceding equation. Before or after a horizontal saccade, perceptual change in spatial localization is not homogeneous across spatial loci and is accompanied by a vertical component.^{2,3} If spatial mislo-

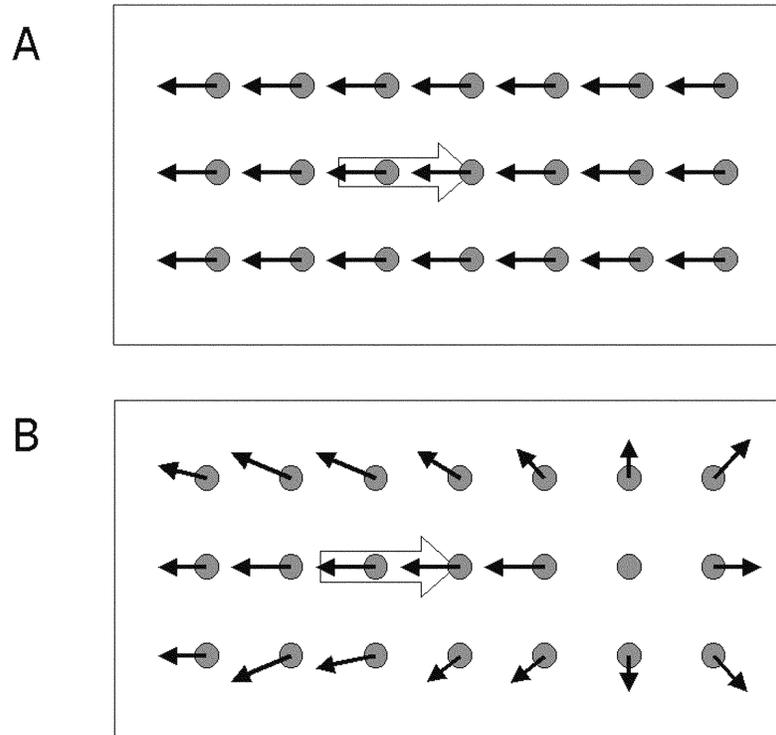


FIGURE 3. Predictions of the subtraction scheme. (A) Pattern of spatial mislocalization predicted by the subtraction scheme: after a rightward horizontal saccade (*open arrow*), localization of each target (*small circles*) involves a constant error in the horizontal direction. (B) Schematic summary of the two-dimensional pattern of localization error as indicated by small arrows.³ Note that after a horizontal saccade, localization error is not homogeneous across visual space and contains a vertical component.

calization immediately after a saccade reflects the subtraction of (damped) EEPS, then the saccadic effect should be homogeneous across the visual field, irrespective of differences in target location, because the EEPS would be in the same direction and of the magnitude for every equivalent eye movement with the relative timing of target presentation controlled. Furthermore, the EEPS representing a horizontal eye movement would not have a vertical component (FIG. 3). Therefore, the process recovering visual stability across a saccade is clearly not characterized by the algebraic subtraction of an extraretinal eye position signal from the retinal information, as pointed out by others.⁶

Similarly, the results that the perceived direction of visual motion in the vicinity of a saccade is biased in the direction opposite to the saccade are counterintuitive under the subtraction scheme, because the extraretinal signal would compensate retinal image motion in the direction of a saccade, not in the direction opposite to it. Saccadic eye movements enhance neural activity in the primate middle temporal area,

which is known to be critically involved in motion perception,⁷ when they cause retinal image flow in the cell's preferred direction.⁸ The predicted perceptual error in perception of direction based on the assumption that the perceived direction is a vector average of the retinal image flow and saccade is inconsistent with the experimental findings. Thus, simple subtraction of a saccade vector from the retinal motion vector to explain the perceived direction is incompatible with the findings.

Physiological studies in the visual cortex have documented changes in neural activities as early as V1 at the time of saccadic eye movements.^{9–11} Recent results from our lab show that the orientation tuning of the cat visual cortex measured immediately after saccades shifts in the direction of saccades.¹² This may underlie perceptual bias in motion direction in the direction opposite to saccade, because "motion streak" signals coding motion direction¹³ are related to the orientation specificity of neurons.¹⁴

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REFERENCES

1. ROSS, J., M.C. MORRONE, M.E. GOLDBERG & D.C. BURR. 2001. Changes in visual perception at the time of saccades. *Trends Neurosci.* **24**: 113–121.
2. KAISER, M. & M. LAPPE. 2004. Perisaccadic mislocalization orthogonal to saccade direction. *Neuron* **41**: 293–300.
3. CHO, S. & C. LEE. 2003. Expansion of visual space after saccadic eye movements. *J. Vis.* **3**: 906–918.
4. PARK, J., J. LEE & C. LEE. 2001. Non-veridical visual motion perception immediately after saccades. *Vision Res.* **41**: 3751–3761.
5. LEE, J. & C. LEE. 2004. Changes in visual motion perception before saccadic eye movements. *Vis. Res.* In press.
6. BRIDGEMAN, B., A.H.C. VAN DER HEIJDEN & B.M. VELICHKOVSKY. 1994. A theory of visual stability across saccadic eye movements. *Behav. Brain Sci.* **17**: 247–292.
7. SALZMAN, C. D., K.H. BRITTEN & W.T. NEWSOME. 1990. Cortical microstimulation influences perceptual judgements of motion direction. *Nature* **346**: 174–177.
8. BAIR, W. & L.P. O'KEEFE. 1998. The influence of fixational eye movements on the response of neurons in area MT of the macaque. *Vis. Neurosci.* **15**: 779–786.
9. TOYAMA, K., M. KIMURA & Y. KOMATSU. 1984. Activity of the striate cortex cells during saccadic eye movements of the alert cat. *Neurosci. Res.* **1**: 207–222.
10. PARK, J. & C. LEE. 2000. Neural discharge coupled to saccade offset in the cat visual cortex. *NeuroReport* **11**: 1661–1664.
11. SUPER, H., C. VAN DER TOGT, H. SPEKREIJSE & V.A. LAMME. 2004. Correspondence of presaccadic activity in the monkey primary visual cortex with saccadic eye movements. *Proc. Natl. Acad. Sci. USA* **101**: 3230–3235.
12. HWANG, J. C. & C. LEE. 2004. Post-saccadic orientation selectivity of neurons in the cat visual cortex. Presented at the 34th Annual Meeting of the Society for Neuroscience Annual Meeting. San Diego, CA, October 27. Program No. 986.5.
13. GEISLER, W.S. 1999. Motion streaks provide a spatial code for motion direction. *Nature* **400**: 65–69.
14. GEISLER, W.S., D.G. ALBRECHT, A.M. CRANE & L. STERN. 2001. Motion direction signals in the primary visual cortex of cat and monkey. *Vis. Neurosci.* **18**: 501–516.